

Differential effects of flower feeding in an insect host–parasitoid system

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Abstract

In many insect host–parasitoid systems, both the host and its parasitoids forage on shared floral resources. As a result of insect behaviour, morphology and physiology, flower species may act selectively at different levels of such systems, e.g., between the trophic levels of hosts and parasitoids, between species within a guild, between sexes or individuals within a species or between life history traits within an individual. We asked if effects of selectivity are consistent across levels in the horse chestnut leafminer, *Cameraria ohridella*, and its parasitoid complex. Insects were exposed singly in no-choice feeding trials to twelve common flower species and their survival and reproduction were recorded. Only one of twelve flower species (*Ranunculus acris*) tended to selectively favour the longevity of leafminers, but not of parasitoids. No flower species were found to favour parasitoids only. Both trophic levels profited from feeding on *Anthriscus sylvestris*, however, parasitoids benefited up to eight times more than their hosts. No differences were found among the species of the parasitoid guild, but females lived significantly longer than males, and single individuals within species were able to exploit generally unfavourable flower species. Out of the seven flower species that increased the longevity of leafminer females, only *Chaerophyllum hirsutum* significantly enhanced the number of eggs laid. Fecundity was generally positively correlated with longevity of leafminer females, but two flower species (*C. hirsutum*, *Taraxacum officinale*) had an additional positive effect on fecundity. In conclusion, we demonstrated that flowers act differently on life history traits in a host–parasitoid system at a multitude of biological levels and that these effects are not always consistent across levels. Selective plant-derived resources can therefore modify herbivore–natural enemy interactions in ways that are more complex than currently appreciated.

Zusammenfassung

Viele herbivore Insekten und ihre Parasitoide nutzen dieselben Blütenarten für die Nektar- und Pollenaufnahme. Unterschiede im Verhalten, der Morphologie und der Physiologie der Insekten können dazu führen, dass solche gemeinsamen Nahrungsquellen das Wirts-Parasitoiden-System auf verschiedenen biologischen Stufen, wie z.B. auf verschiedenen trophischen Ebenen, zwischen den verschiedenen Arten einer Gilde, zwischen Individuen respektive Geschlechtern einer Art oder zwischen Komponenten der Lebenszyklusstrategie eines Individuums, unterschiedlich beeinflussen. Für die Roskastanienminiermotte (*Cameraria ohridella*) und ihren Parasitoidenkomplex wurde in dieser Studie untersucht, ob der Einfluss unterschiedlicher Blütenarten über verschiedene Stufen konsistent ist. Dazu wurde

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die Überlebensdauer und Reproduktion von Miniermotten und Parasitoiden auf mehreren Blütenarten ermittelt. Nur eine der zwölf getesteten Blütenarten (*Ranunculus acris*) zeigte eine Tendenz, das Überleben von *C. ohridella* gegenüber ihren Parasitoiden selektiv zu fördern. Obwohl alle getesteten Insektenarten auf *Anthriscus sylvestris* länger überlebten, profitierten Parasitoide gegenüber ihren Wirten achtmal mehr. Auf der trophischen Ebene der Parasitoiden konnten keine Unterschiede zwischen den einzelnen Arten ermittelt werden, jedoch lebten Parasitoidenweibchen signifikant länger als Männchen und einzelne Individuen waren in der Lage, allgemein wenig geeignete Blütenarten zu nutzen. Von den sieben Pflanzenarten, die das Überleben von *C. ohridella* förderten, erhöhte einzig *Chaerophyllum hirsutum* die Anzahl gelegter Eier pro Weibchen. Generell korrelierten Lebensdauer und Fruchtbarkeit der Blattminiererweibchen positiv miteinander. *Chaerophyllum hirsutum* und *Taraxacum officinale* hatten ferner einen positiven Einfluss auf die Fruchtbarkeit. Insgesamt konnten wir zeigen, dass Blüten auf verschiedenen Stufen die Komponenten der Lebenszyklusstrategie eines Wirts-Parasitoiden-Systems unterschiedlich beeinflussen können und dass die Effekte über die einzelnen Stufen nicht immer konsistent sind. Selektive Blütenressourcen können daher Interaktionen zwischen Herbivoren und ihren natürlichen Feinden auf komplexere Art und Weise modifizieren als allgemein angenommen.

Keywords: Selectivity; Floral resources; Trophic interactions; Conservation biological control

Introduction

Floral and extrafloral nectar and pollen are essential sources of carbohydrates and proteins for many non-pollinating insects and are therefore crucial for their fitness (Jervis & Kidd, 1996; Van Driesche & Bellows, 1996). Many studies have shown that access to these floral resources increases survival and reproduction of insects (e.g., Berndt & Wratten, 2004; Leius, 1961; Wäckers, van Rijn, & Bruin, 2005; Wade & Wratten, 2007). A combination of factors determines the value of a flower species as a food source. The effect of flowers on the fitness of insects varies with nutrient composition and morphological characteristics of the plant (Baker & Baker, 1983; Idris & Grafius, 1995). In addition, body size and mouthpart morphology of consumers in combination with flower morphology may exclude or restrict access to food resources (Patt, Hamilton, & Lashomb, 1997). Thus, flower species are not equally accessible and of the same nutritional value to the many insect guilds.

In insect host–parasitoid systems where both, the host and its parasitoids, forage on floral resources and thus increase their survival and reproductive success, selectivity of flowers may favour one trophic level (or species within a trophic level) over the other. This applies, for example, to the great majority of lepidopteran hosts and their hymenopteran and dipteran parasitoids. Herbivores and their parasitoids differ in the morphology of their mouthparts and probably also in their nutritional requirements and may therefore be differentially affected by resources in their common environment. However, a selective effect of flower species at one level may not necessarily translate into an effect at the population level; counteractive effects at other levels may mitigate or even outweigh these former effects. For

example, flower species providing nectar that extends a consumers' lifetime may not necessarily be attractive, and flowers, which show a high degree of attractiveness, may not always increase consumers' fitness (Wäckers, 2004). Moreover, flower species may be more favourable for a particular species within a guild, for a particular sex, for a few individuals or for particular life history traits within a species. The availability and identity of selective floral resources may therefore have major consequences for the population dynamics of host–parasitoid systems (Baggen & Gurr, 1998; Begum, Gurr, Wratten, Hedberg, & Nicol, 2006; Kean, Wratten, Tylianakis, & Barlow, 2003; Tylianakis, Didham, & Wratten, 2004; Wäckers, Romeis, & Van Rijn, 2007). However, while selective effects of floral resources at individual levels have been shown in several studies, it is unknown whether selectivity acts specifically on different levels in herbivore–parasitoid systems and which levels are important. To date, studies on flower selectiveness at levels other than the guild are rare (e.g. Wäckers, 2004). This lack of knowledge and awareness may be one of the major reasons why the success of increased nectar supply in conservation biological control has been variable and is difficult to predict (Baggen, Gurr, & Meats, 1999; Winkler, 2005).

The goal of this paper was to study selective effects of floral food sources at different biological levels in a multitrophic system consisting of the horse chestnut leafminer, *Cameraria ohridella* Deschka and Dimic (Lepidoptera, Gracillariidae), and its most abundant parasitoids *Minotetrastichus frontalis* Nees, *Phygadeuon* sp. and *Chrysocharis* sp. (Hymenoptera: Eulophidae; Kehrli, Lehmann, & Bacher, 2005). With this study we aim to investigate if effects of selectivity at one level can be predicted from

other levels. The following specific questions were addressed:

- (1) Do flower species have different effects on the fitness of parasitoids and their hosts?
- (2) Are there differences in the food suitability between species of the parasitoid guild, between sexes, or between individuals within a species?
- (3) Do flowers have contrasting effects on life-history traits such as longevity or fecundity?
- (4) Can food sources have an effect on reproduction, which goes beyond their impact on longevity?
- (5) Are effects consistent across levels?

Material and methods

Study system

C. ohridella is a recently introduced, highly invasive pest of unknown origin that has spread over large parts of Europe during the last 15 years. It frequently defoliates white flowering horse chestnut trees (*Aesculus*

hippocastanum L., Hippocastanaceae) already in summer (reviewed by Heitland, Kopelke, Freise, & Metzger, 1999). Even though several native parasitoids, mostly generalist chalcidoid wasps, are known to develop on *C. ohridella*, they are not able to regulate the leafminer population. Therefore great efforts were made to augment and conserve the native parasitoid population (Kehrli et al., 2005). However, the access of resident and released parasitoids to carbohydrates might be limited in urban areas and the provision of floral resources under horse chestnut trees was considered (Heitland et al., 1999). Potential flower species should ideally bloom early in the season to target parasitoids attacking the first leafminer generation and should be tolerant to nutrient input and shading. We used the native plant species listed in Table 1, all of which have been reported to provide nectar and/or pollen (Jervis, Kidd, Fitton, Huddleston, & Dawah, 1993; Kühn, Durka, & Klotz, 2004).

Source of insects and plants

In autumn, *C. ohridella*-infested horse chestnut leaf litter, which also contained pupae of the overwintering

Table 1. Impact of food sources on the longevity of *C. ohridella* and its parasitoids *Chrysocharis* sp., *M. frontalis* and *P. agraulles*

Food source	<i>C. ohridella</i>		<i>Chrysocharis</i> sp.		<i>M. frontalis</i>		<i>P. agraulles</i>	
	Sucrose ^a	Water ^b	Sucrose ^a	Water ^b	Sucrose ^a	Water ^b	Sucrose ^a	Water ^b
Apiaceae								
<i>Aegopodium podagraria</i> L.	ns	+++	–	++				
<i>Anthriscus sylvestris</i> Hoffm.	ns	++	ns	+++	ns	+++	ns	+++
<i>Chaerophyllum hirsutum</i> L.	ns	+						
Brassicaceae								
<i>Alliaria petiolata</i> [Bieb.] Cavara & Grande	ns	++						
<i>Cardamine pratensis</i> L.	ns	+			---	+		
Ranunculaceae								
<i>Ranunculus acris</i> L.	ns	+			---	ns		
<i>Ranunculus ficaria</i> L.	ns	++			---	+		
Fabaceae								
<i>Medicago sativa</i> L.	–	ns			---	ns		
Geraniaceae								
<i>Geranium robertianum</i> L.	--	ns	---	ns	---	ns		
Dipsacaceae								
<i>Knautia arvensis</i> (L.) Coulter	---	ns			---	ns		
Asteraceae								
<i>Taraxacum officinale</i> Weber	---	ns	---	ns	---	ns		
<i>Bellis perennis</i> L.	--	ns	---	ns	---	ns	---	ns

Minus signs indicate that the longevity on the particular food source was significantly lower than on 1 M sucrose solution, plus signs indicate that the longevity on the particular flower was significantly higher than on water (Fisher's LSD *post-hoc* tests).

^a(ns) not significant; – $P \leq 0.05$; -- $P \leq 0.01$; --- $P \leq 0.001$.

^b(ns) not significant; + $P \leq 0.05$; ++ $P \leq 0.01$; +++ $P \leq 0.001$.

parasitoids, was collected in Bern, Switzerland, and stored until the next spring at 5 °C and L/D 8/16 h in a climate chamber. For emergence of all leafminers and parasitoids, the stored leaf litter was incubated at L/D 14/10 h and 20/12 °C. Emerged insects were identified within 24 h and thereafter used immediately for the set-up of experimental trials.

Flowers of plant species tested (Table 1) were collected at natural stands around Bern. The stalks of freshly cut flowers were placed in water-filled plastic vials ($\varnothing = 3.4$ cm, $h = 8$ cm) and the vials were plugged with rubber foam to avoid drowning of insects (see Wade & Wratten, 2007). Flowers were used within 3 h for the experimental trials and assigned randomly to species and sex of the emerging insects.

Assessment of the longevity and fecundity of leafminers

Upon emergence, female and male *C. ohridella* were kept together for 2 days to allow mating. Thereafter, the food-deprived 2-day-old females were transferred into transparent plastic cylinders ($\varnothing = 11$ cm, $h = 15.5$ cm), where they were kept singly for the rest of their lifetime in no-choice feeding trials. The cylinders were sealed on top with gauze mesh, a filter paper covered the bottom and a water moistened sponge was provided. Females of *C. ohridella* were tested on one of 14 different resources. Either they were kept on one of the 12 species of cut flowers, on water or on 1 M sucrose solution (Table 1). The sucrose treatment was used as a high-energy control whereas the water treatment served as a low-energy control. The water treatment consisted of a water-filled plastic vial closed with soaked rubber foam. In the sucrose treatment a 1 M sucrose saturated sponge ($V \approx 1$ cm³) was offered additionally to a water-filled vial. Different food sources were vertically placed in the middle of the cylinders and were replaced every 4 days or earlier if they had become spent. Each female was reared on a single type of food source over its whole lifetime. To investigate their fecundity, *C. ohridella* females were presented fresh uninfested horse chestnut leaf discs (5 cm²) every day to stimulate oviposition and to allow egg deposition.

The individuals tested were checked daily and survival as well as the number of eggs laid on the leaf discs was recorded; females, which did not survive the first day in the cylinder, were excluded from the analysis. Fecundity is here defined as the total number of eggs laid on the leaf discs or on the cylinder wall. All trials were carried out in the same climate chamber under standardized conditions (L/D: 14/10 h and 20/12 °C). For each treatment a minimum of 15 replicates were conducted.

Assessment of the longevity of parasitoids

Food-deprived, unmated, freshly emerged individuals of *M. frontalis*, *P. agraulis* and *Chrysocharis* sp. were identified, sexed (except *Chrysocharis* sp. in which the sexes could not be discriminated) and then transferred to transparent plastic cylinders of the same type as described above, where they were kept singly in no-choice trials for the rest of their lifetime. Due to the small number of parasitoids that emerged, each of the three species was only tested on a subset of flower species: *M. frontalis*, *P. agraulis* and *Chrysocharis* sp. were exposed to nine, two and five flower species, respectively. Overall, parasitoids were tested on 10 of the 12 flower species summarized in Table 1. Food sources were offered in the same way as described above and each individual was reared on a single type of food source over its whole lifetime.

Trials were conducted in the same climate chamber and under the same standardized conditions (L/D: 14/10 h and 20/12 °C) as the assessments of the leafminer. Each treatment was replicated between 5 and 12 times. Parasitoids were checked daily and survival was recorded; individuals who died on the first day were excluded from analysis.

Statistical analysis

Insect species were analysed separately. Females of *C. ohridella* that laid no eggs were excluded from analyses of fecundity data in order to exclude malformed females and potential incorrect sexing. Otherwise, adult longevity (days of adult survival) and fecundity (number of eggs laid) were square-root or log transformed prior to analysis and treated as dependent variables whereas food source and sex were treated as nominal independent variables. Dependent variables were analysed separately by a one-way ANOVA for *Chrysocharis* sp. and *C. ohridella* (with food source as the only independent variable) whereas *M. frontalis* and *P. agraulis* were analysed by two-way ANOVAs (food source and sex as independent variables). Means within food sources were pairwise compared by the liberal but consistent Fisher's LSD *post-hoc* test, which also accounts for the different numbers of treatment levels (Zar, 1996).

To detect plasticity in flower usage within insect species, parasitoids' longevity was fitted to a Poisson distribution, with λ being the species' mean longevity on the particular food source. We then calculated for each individual parasitoid the probability of belonging to the Poisson distribution.

The dependence of *C. ohridella*'s fecundity upon the longevity and additional direct effects of flower species (food sources were dummy coded, base = water treatment) were analysed by a backward stepwise regression. The fulfilment of the model assumptions

were checked by visual inspection of the distribution of residuals for every statistical test conducted.

Results

Do flower species have different effects on the fitness of parasitoids and hosts?

The 14 food sources differed significantly with regard to their impact on the longevity of all insects tested (Table 2). Flowering species tested of the families Asteraceae, Dipsacaceae, Fabaceae and Geraniaceae did not increase the longevity of the herbivore or its parasitoids compared to the water control. However, both parasitoids and hosts benefited from the supply of *Anthriscus sylvestris*, *Aegopodium podagraria*, *Cardamine pratensis* and *Ranunculus ficaria* (Table 1, Figs. 1A and 2). Although the latter three flower species enhanced parasitoid survival compared to the water control, they were significantly inferior to the high-energy control sucrose or *Anthriscus* (Table 1, Fig. 2). *Ranunculus acris* was the only floral resource showing a minor selective effect on the two guilds (Table 1): leafminer females lived slightly longer when they were fed on *R. acris* compared to the water control (Fig. 1) whereas *M. frontalis*, the only parasitoid tested on this flower species, did not benefit (Fig. 2B). No plant species tested was beneficial only to parasitoids (Table 1). However, *Anthriscus* enhanced the longevity of natural enemies between 8.2 and 11.8 times compared to the water treatment, whereas the leafminers lived only 1.4-times longer.

Table 2. ANOVA tables on the impact of food source and sex on the longevity of the leafminer *C. ohridella* and its parasitoids *Chrysocharis* sp., *M. frontalis* and *P. agraulæ*

Source of variance	df	Sum of Sq	F value	P
<i>C. ohridella</i>				
Food source	13	11.21	3.86	<0.001
Error	223	49.88		
<i>Chrysocharis</i> sp.				
Food source	6	8.99	24.72	<0.001
Error	62	3.76		
<i>M. frontalis</i>				
Food source	10	19.95	21.31	<0.001
Sex	1	1.96	20.97	<0.001
Food source × sex	10	1.19	1.27	0.253
Error	186	17.42		
<i>P. agraulæ</i>				
Food source	3	19.87	213.82	<0.001
Sex	1	0.22	7.16	0.010
Food source × sex	3	0.38	4.13	0.010
Error	61	1.89		

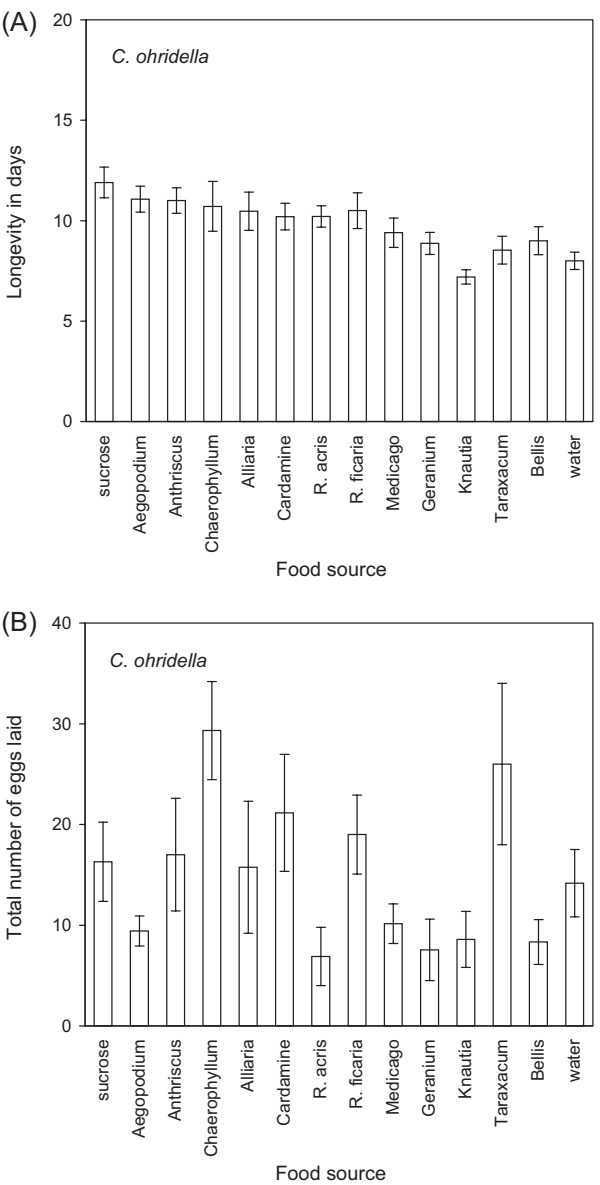


Fig. 1. Effect of food sources (genus names refer to flower species tested) on (A) the longevity and (B) the fecundity of *C. ohridella* females. Data are untransformed, bars = 1 SE.

Are flowers differentially suitable within and among parasitoid species?

No differences in food suitability within the parasitoid guild were found. All three species lived significantly longer when they were kept on *Anthriscus* or sucrose compared to all other food sources tested (Table 1, Fig. 2). However, females of *M. frontalis* and *P. agraulæ* lived significantly longer than males (Table 2, Fig. 2). Females and males of *M. frontalis* had the same food requirements. By contrast, females of *P. agraulæ* benefited more from the sucrose solution than their males as indicated by the significant interaction term of

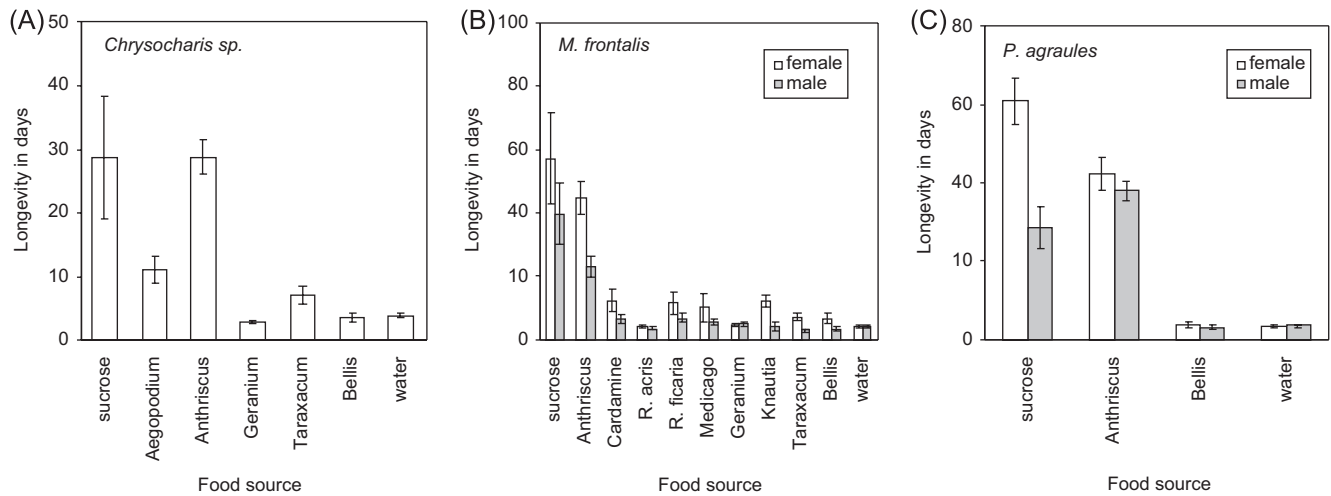


Fig. 2. Effect of food sources (genus names refer to flower species tested) on the longevity of (A) *Chrysocharis* sp., (B) *M. frontalis* and (C) *P. agraulis*. Data are untransformed, bars = 1 SE.

food source and sex (Table 2, Fig. 2C). Additionally, outliers in the box plots (Fig. 3) represent single females of *M. frontalis* that were able to exploit *Cardamine* (Poisson distribution: $\lambda = 9.650$, $P_{(X \geq 42 \text{ days})} < 0.001$), *R. ficaria* ($\lambda = 9.875$, $P_{(X \geq 40 \text{ days})} < 0.001$), *Medicago sativa* ($\lambda = 7.810$, $P_{(X \geq 50 \text{ days})} < 0.001$), or *Bellis perennis* ($\lambda = 5.333$, $P_{(X \geq 16 \text{ days})} < 0.001$).

Do flower species have contrasting effects on different life-history traits?

The different food sources also had significant effects on the leafminers' fecundity ($F_{13,158} = 2.37$, $P = 0.024$). *C. ohridella* females feeding on *Chaerophyllum hirsutum* laid significantly more eggs than females held on sucrose (Fisher's LSD: $P = 0.014$) or water (Fisher's LSD: $P = 0.011$) (Fig. 1B). Moreover *Chaerophyllum* was significantly superior to all other treatments except *Cardamine*, *R. ficaria* and *Taraxacum officinale*. The sucrose control did not increase the fecundity of *C. ohridella* compared to the water control and the fecundity in no other treatment differed significantly from these two control treatments (Fig. 1B). Thus, whereas *Aegopodium*, *Anthriscus*, *Alliaria petiolata*, *Cardamine*, *R. acris* and *R. ficaria* enhanced the longevity of females compared to the water treatment (Table 2) they had no effect on fecundity. Therefore, *Chaerophyllum* was the only flower which significantly enhanced both longevity and fecundity of *C. ohridella*.

Do flower species have a direct effect on reproduction?

Analysing the dependence of reproduction upon flower species and females' survival, backward stepwise regression revealed that the fecundity of *C.*

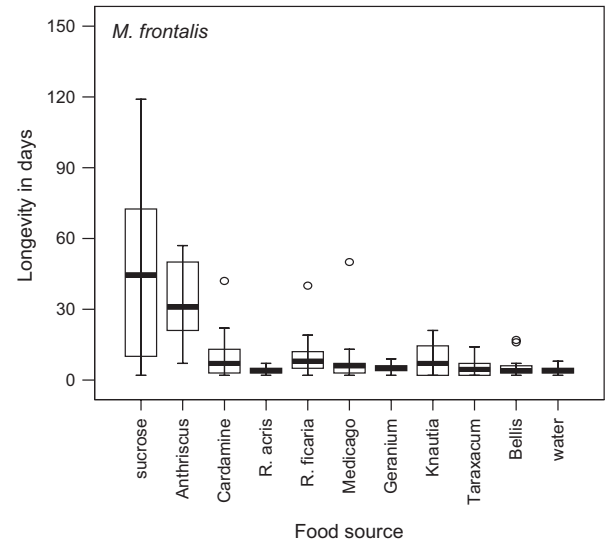


Fig. 3. Boxplot of the effect of food sources (genus names refer to flower species tested) on longevity of *M. frontalis*. Data are untransformed, circles represent values that were more than 1.5 box lengths from the edge of the box.

ohridella was highly positively related to longevity and two flower species; *Chaerophyllum* and *Taraxacum* had an additional direct positive effect on reproduction, which went beyond the increase of longevity (Table 3).

Discussion

Our results clearly revealed (1) that flowers act differently on life history traits of herbivores and their parasitoids at a multitude of biological levels, (2) that

Table 3. Backward stepwise regression on the dependence of *C. ohridella*'s fecundity upon lifetime and food sources; females that laid no eggs were excluded for analysis

Independent variable	Coefficient	Std. error	t value	P
Constant	0.476	0.921	0.517	0.606
Longevity	0.836	0.292	2.863	0.005
<i>Chaerophyllum hirsutum</i>	1.809	0.612	2.959	0.004
<i>Cardamine pratensis</i>	0.908	0.506	1.796	0.074
<i>Ranunculus acris</i>	-0.977	0.601	-1.627	0.106
<i>Ranunculus ficaria</i>	0.910	0.599	1.520	0.131
<i>Taraxacum officinale</i>	1.554	0.550	2.828	0.005

The $\sqrt{\cdot}$ -transformed fecundity was treated as the dependent variable, whereas the $\sqrt{\cdot}$ -transformed longevity of the females and the dummy coded food sources (base = water treatment) served as independent variables. Significant *P* values are shown in bold typface. Residual standard error: 1.731 on 165 df, Multiple *R*- Squared: 0.1695, *F*-statistic: 5.614 on 6 and 165 df, the *P* value is 0.00002515.

the outcome differs between species and (3) that not all effects point in the same direction.

In our experiment, females of *C. ohridella* had an increased longevity when feeding on flowers of the families Apiaceae, Brassicaceae and Ranunculaceae, but not on other plant families. However, only *Chaerophyllum* additionally enhanced the fecundity of leafminers. Flowers can therefore have selective effects on different life history traits of insects (Baggen & Gurr, 1998; Baggen et al., 1999; Leijs, 1961). The ecological and physiological ways by which food resources affect longevity, egg production and consequently the reproductive success of females are only partly understood (Casas et al., 2005). It is often assumed that the reproduction of insects mainly depends on the longevity of females (Baggen & Gurr, 1998; Leather, 1984; Proshold, Karpenko, & Graham, 1982). This was also the case in our study, as *C. ohridella* females that lived longer generally laid more eggs. However, feeding on carbohydrates can help insects to mature additional eggs and can prevent females from resorbing eggs (Heimpel, Rosenheim, & Kattari, 1997; Olson & Andow, 1998). Thus, floral resources could have a direct effect on insect reproduction, which goes beyond increasing lifespan. In our study, the two flower species *Chaerophyllum* and *Taraxacum* directly increased the fecundity of the leafminer, demonstrating that floral resources like *Chaerophyllum* can directly affect both the survival as well as the fecundity of insects or, as in the case of *Taraxacum*, primarily the fecundity. The reasons why *Chaerophyllum* and *Taraxacum* were particularly favourable for the reproductive success of leafminers are unknown. Future research should examine the sugar, amino acid, protein and lipid composition of *Chaerophyllum* and *Taraxacum*'s nectar and pollen. Overall, our finding emphasizes that single fitness measurements may give an incomplete picture of the

effects of floral resources on natural enemies and their herbivorous prey. Investigations of single fitness measures can therefore be misleading and consequently the common practice of using longevity as a proxy for lifetime fecundity in insects may not always be justified.

The flower species tested also differed in their impact on the longevity of the three parasitoid wasp species. All three species lived longer on flowers of the families Apiaceae, Brassicaceae and on *R. ficaria*, similar to the results in the host species. In accordance with other studies (Charleston, Kfir, Dicke, & Vet, 2005; Van Lenteren, Van Vianen, Gast, & Kortenhoff, 1987) we found that females of *M. frontalis* and *P. agraulles* generally lived longer than males. However, our findings also indicate that sucrose, which is together with its hexose components glucose and fructose, the most prevalent sugar in nectar (Baker & Baker, 1983), nurtured the two sexes of *P. agraulles* differently. Thus, different types of sugar do not only differently affect the fitness of parasitoids in general (Wäckers, 2001), they might even differ in their effect on the two sexes. In addition, individual *M. frontalis* females seemed to be able to feed on generally unfavourable flower species such as *Cardamine*, *R. ficaria*, *Medicago* and *Bellis*. Differences of up to 40 days to the mean longevity on these flower species are unlikely an artefact of variation among the flowers provided because the flowers were frequently replaced. A similar plasticity within species was also observed by Wäckers (2004) in the weight gain of parasitoids from floral resources. Even though this plasticity to a food source may only marginally affect the population average of an insect species, it might have ecological consequences by affecting population structure and exploitation of micro-niches (Miner, Sultan, Morgan, Padilla, & Relyea, 2005).

Focusing on the guild of parasitoids, we detected no differences in the exploitation of floral resources among *Chrysocharis* sp., *M. frontalis* and *P. agraulles* on the subset of flowers tested with multiple parasitoids. All three parasitoid species were unaffected by the provision of *Bellis* and benefited from *Anthriscus*. In line with previous studies (Schmale, Wäckers, Cardona, & Dorn, 2001; Wäckers, 2004) it appears that certain generalizations are possible with respect to the suitability of flowers as food resources for parasitoids. However, it should be noted that the parasitoids in our study were all from the same subfamily (Eulophinae), all parasitize leafminers and were all of similar body size. More distantly related parasitoids or species occupying different ecological niches may differ in their food requirements (Lavandero, Wratten, Didham, & Gurr, 2006).

Only one out of ten flower species tested seemed to be exploited by the herbivore but not its natural enemies: leafminers lived slightly longer when kept on *R. acris* whereas the survival of *M. frontalis*, the only parasitoid species tested on this plant species, was not affected. On the other hand, we found no flower species

that only benefited natural enemies. However, the parasitoids benefited up to eight times more from the provision of flowers of *Anthriscus* than their host. Thus, even flower species that are beneficial to both trophic levels may be able to act selectively by favouring parasitoids more than their hosts (Wäckers et al., 2007; Winkler, Wäckers, Stingli, & van Lenteren, 2005). This may have important consequences for the population dynamics in the system, as the synovigenic parasitoids are allowed more time to mature their eggs, which may eventually lead to enhanced parasitism rates and thus a stronger suppression of the host population (Winkler, Wäckers, Bukovinszky-Kiss, & van Lenteren, 2006). By contrast, a selective flower species such as *R. acris*, which slightly enhanced the survival, but not the reproduction of leafminers, will probably have little to no effect on the population dynamics in the system. These findings emphasize the importance of studying not only the direction but also the magnitude of effects of floral resources in order to assess their impact on population dynamics.

In conclusion, we demonstrated that flower species can selectively affect a host–parasitoid system at multiple levels simultaneously. Selectivity in flowers has therefore direct implications for applied fields like conservation biological control. Our results challenge the current practice of provisioning unscreened wild-flowers to attract, conserve and augment natural enemies for pest control (e.g. Rebek, Sadof, & Hanks, 2006; Wyss, 1995). Even though all the flower species tested in this study matched habitat requirements and were all providing nectar and/or pollen accessible to the insects (Kühn et al., 2004), our screening revealed that most of the candidates tested are probably unsuitable for a conservation biological control approach against *C. ohridella*. Moreover, the attractiveness of a potential candidate such as *A. sylvestris* has still to be demonstrated. Nonetheless, our results suggest that only careful screening for suitable flower species in the laboratory followed by rigorous field trials enhances the success of flower provisioning in conservation biological control. In general, our work emphasizes the importance of multitrophic investigations for understanding the consequences of shifts in plant-derived food resources on herbivore–natural enemy interactions. Only the understanding of cascading effects alone and in concert will provide insight into multitrophic interactions and thereby allow for predicting the outcome of management regimes.

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